

TRAIL COMMUNICATION IN THE DACETINE ANT  
*ORECTOGNATHUS VERSICOLOR*  
(HYMENOPTERA: FORMICIDAE)\*

BY BERT HÖLLDOBLER

Department of Organismic and Evolutionary Biology,  
Harvard University, Cambridge, Mass. 02138

Although division of labor within two dacetine species has been studied at length (Wilson 1962; Carlin 1982), very little has hitherto been reported on social communication in the Dacetini, a myrmicine tribe of nearly 200 known species (Brown and Wilson 1959; Wilson 1962). Foraging habits have also been studied in several species (for review see Brown and Wilson 1959; Wilson 1962). As now known, the dacetines seem to be individual foragers; recruitment to food sources and cooperation during retrieval of prey have not been observed. It is therefore of some interest that we have recently discovered trail laying and trail following in the dacetine species *Orectognathus versicolor*. Experiments in the laboratory further indicate that trail communication may play an especially important role during nest emigrations.

*Material and Methods:*

A queenright colony of *O. versicolor* was collected from rotting wood near Eungella, North Queensland (Australia) and housed in a glass tube ( $\phi$  1 cm), with water trapped at its bottom behind a cotton plug. The nest tube was laced into an arena ( $45 \times 30$  cm) in which small pieces of cockroaches (*Nauphoeta cinerea*), chopped meal worms (*Tenebrio molitor*), several species of small flies and honey water were provided as food. The colony developed very well under these conditions, and when the experiments began (4 weeks after collection) it contained one queen, 80 workers (42 minors, 27 medias, 11 majors (see Carlin, 1982)), 14 freshly eclosed males, and brood of all stages.

For histological investigations live specimens were fixed in Carnoy (Romeis 1948), embedded in methyl-methacrylate and sectioned  $8 \mu$  thick with a Jung Tetrander I microtome (Rathmayer 1962). The

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staining was Azan (Heidenhain). The SEM pictures were taken with an AMR 1000 A scanning electron microscope.

Additional methodological details will be given with the description of the individual experiments.

### Results:

As demonstrated by Carlin (1982) most of the foraging in *O. versicolor* is conducted by the minor and medium worker castes; the majors function primarily or entirely as a defense caste, for which they have unique modifications in the form of the mandibles. Although workers of *O. versicolor* seem to forage individually, our observations in the laboratory indicate that some sort of social facilitation might be involved in stimulating foraging activity in the colony.

Often not more than 1-3 workers roamed the foraging arena. But when suddenly 30-50 flightless *Drosophila* flies were released into the arena, and the first one or two foragers had returned with captured prey to the nest, the number of workers leaving the nest tube and venturing into the foraging arena increased markedly. We did not, however, observe the foragers performing any motor display inside the nest, which might have stimulated the nestmates,



Fig. 1. Part of the colony of *Orectognathus versicolor*, the three worker castes (minors, medias, majors), males, and different developmental stages.

nor did it appear that workers leaving the nest followed chemical trails.

On the other hand, trail following was very obvious when the colony or fragments of the colony were forced to move to a new nest site. For example, when we shook the colony out of the nest tube into the arena, which had been provided with a new papered floor before each experiment, the "homeless" colony soon gathered at one spot, where it was closely guarded by members of the major worker caste (Fig. 1). After varying intervals (sometimes lasting more than one hour), some of the minors and medias began exploring the arena, and eventually they discovered a nest tube that had been provided at the edge of the arena (usually 30–35 cm away from the displaced colony). After exploring the nest tube, some of the ants returned to the colony, and after a while they often moved again to the nest tube to continue to explore it thoroughly.

Usually this procedure was repeated several times, before the first signs of a colony movement could be observed. It occurred when several additional minors and medias departed from the colony and traveled directly to the new nest. Their straight orientation and the fact that during running they kept the tips of their antennae close to the ground, suggested that these ants were following a chemical trail. Soon afterwards the traffic between the "homeless" colony and the newly discovered nest tube increased leading finally to a full-scale colony emigration.

All three worker castes were involved in transporting brood, callow workers, and males to the new nest, although the minors handled eggs and small larvae preferentially while the medias and majors concentrated on large larvae, pupae and adults (Fig. 2). Usually the queen moved during the early phase of the colony movement and always traveled on her own. On the other hand, the males were always carried by the workers (Fig. 2), usually not before most of the brood had already been moved. Only once did we see a fully pigmented worker being carried by a nestmate. The transported individual was grasped dorsally at the head and lifted upwards with gaster tip pointing forwards; it had the appendages folded in the pupal position. All ants traveled along a relatively narrow route between colony and new nest site. This strongly suggested that *O. versicolor* employs chemical trail communication during the process of colony migration. The following experiments

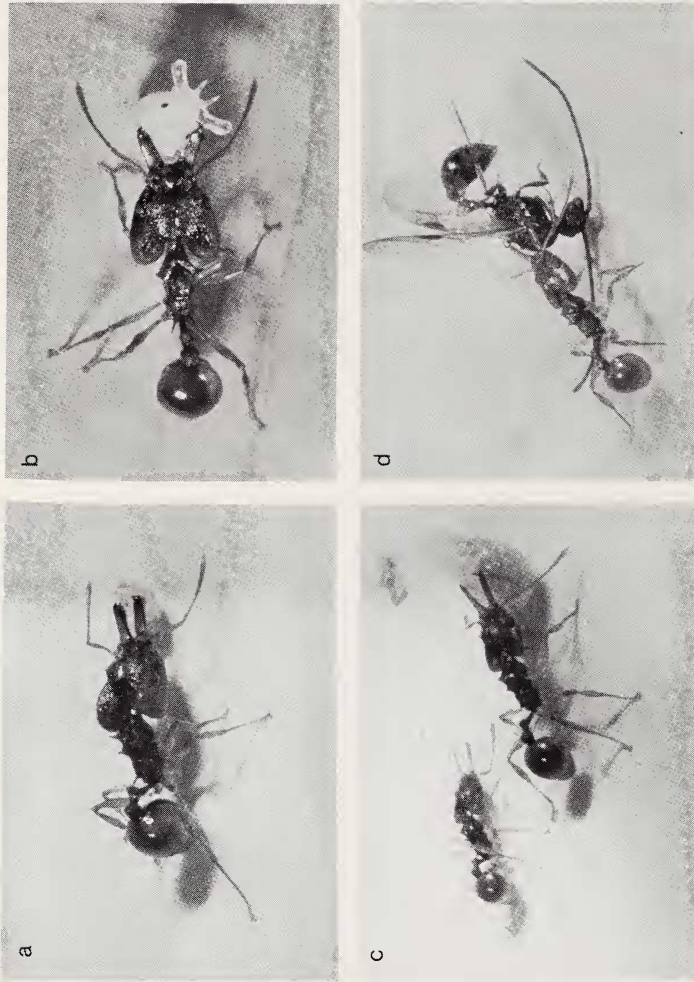


Fig. 2. Colony emigration in *Orectognathus versicolor*. (a) major transporting larva; (b) major transporting pupa; (c) media transporting larva, accompanied by a minor; (d) media transporting male.



were designed to localize the anatomical source of a possible trail pheromone in *O. versicolor*.

Close-up cinematography and photography revealed that many *Orectognathus* workers, when moving back and forth between the displaced colony and the nest tube, touched their abdominal tips intermittently to the ground, presumably depositing droplets of trail pheromone. Three major exocrine glands open at or near the abdominal tip of *O. versicolor* workers: the poison gland and Dufour's gland, both of normal size, and a relatively large pygidial gland, which opens between the 6th and 7th abdominal tergites (Fig. 3).

Most myrmicine ants have a more or less well developed pygidial gland (Hölldobler et al. 1976, Hölldobler and Engel 1978; Kugler 1978), but in *O. versicolor* this gland is more complex than usually found in Myrmicinae. It more closely resembles the pygidial gland of some ponerine species, for example *Pachycondyla laevigata*, in which it serves as the source of a trail pheromone. The paired reservoir sacs (invaginations of the intersegmental membrane between the 6th and 7th tergites) are filled with a clear, lightly brownish liquid. Several ducts lead from paired clusters of glandular cells into the reservoir, penetrating the intersegmental membrane (Fig. 4). The cuticle of the 7th tergite has a grooved structure (Fig. 5), underneath of which is a large glandular epithelium (Fig. 4). *Orectognathus versicolor* workers, when engaged in trail laying behavior, usually hold their gaster in an almost vertical position. This brings the opening of the pygidial gland very close to the floor so that part of the grooved structure on the 7th tergite can be easily put in contact with the surface of the ground.

In the next series of experiments we tested the trail following response of *O. versicolor* to artificial trails drawn with glandular secretions of the poison gland, Dufour's gland and pygidial gland. The glands were dissected out of freshly killed workers and for each trail test one gland of a kind was crushed on the tip of a hardwood applicator stick and smeared once along a 20-cm-long pencil line. The trails were made to originate either from the entrance of the nest tube or from the periphery of the clustered colony, which had previously been shaken out of their nest tube into the test arena. As a control a second trail was offered simultaneously which was derived either from a droplet of water or from one of the other

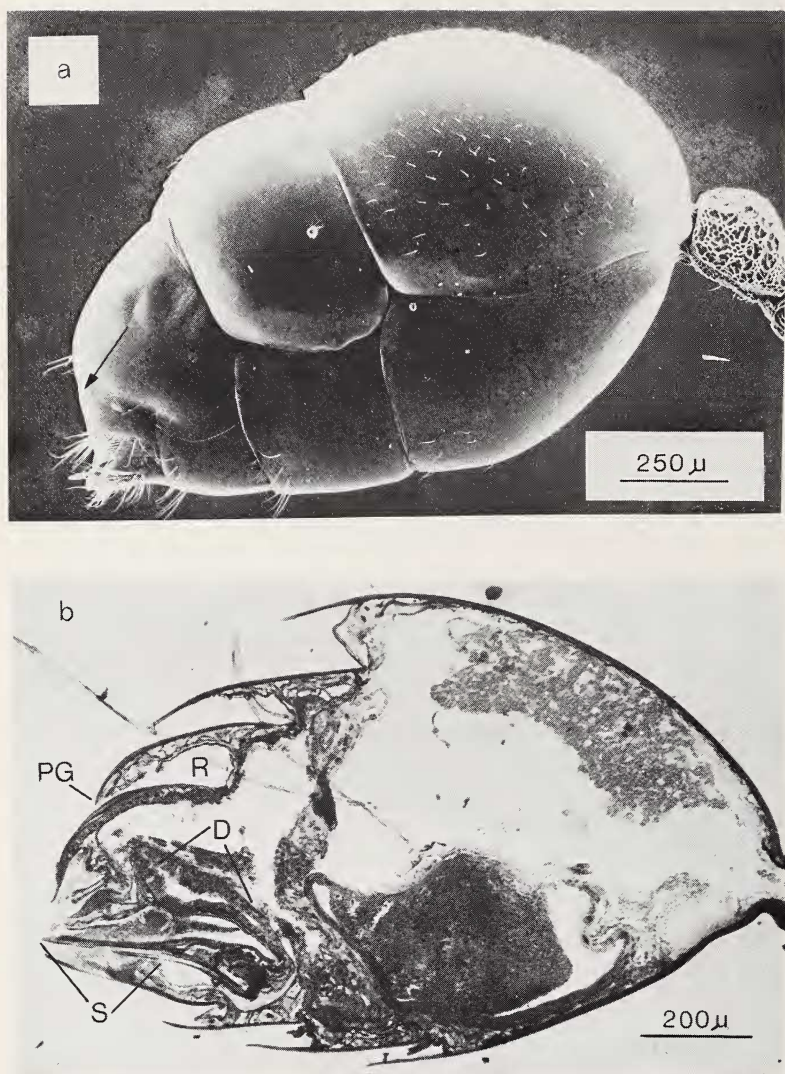


Fig. 3. Gaster of a media of *Orectognathus versicolor*. (a) SEM picture; arrow indicates opening of pygidial gland. (b) Sagittal section through gaster of a media. PG = pygidial gland; R = reservoir of pygidial gland; D = Dufour's gland; S = stinger.

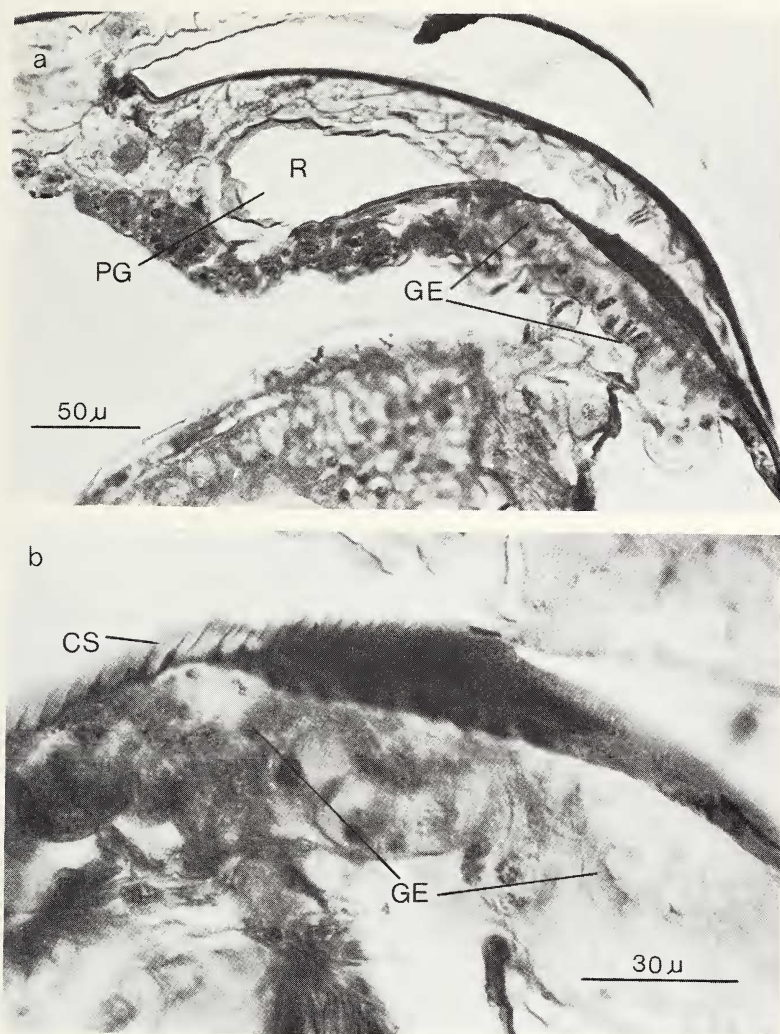


Fig. 4. (a) Sagittal section through pygidial gland of a media of *Orectognathus versicolor*. PG = pygidial gland; R = reservoir of pygidial gland; GE = glandular epithelium. (b) Close-up of glandular epithelium (GE) under the cuticular structure (CS) of pygidium.



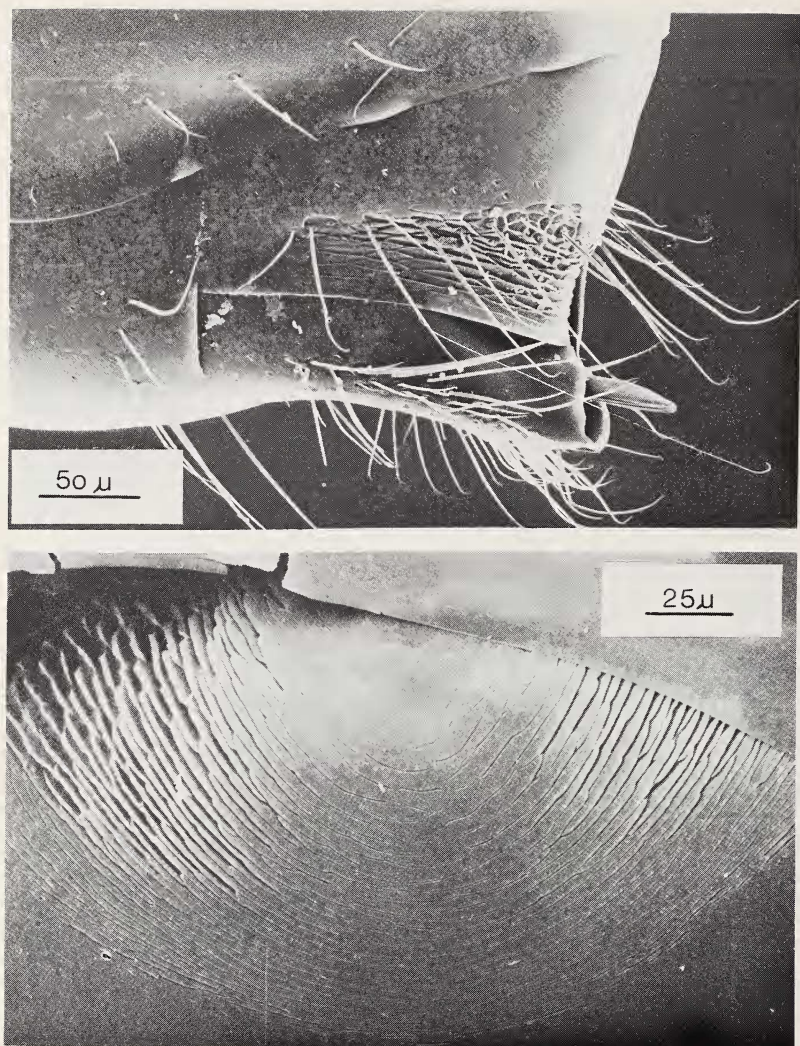


Fig. 5. Above: SEM pictures of the gaster tip of a media of *Orectognathus versicolor*. The slightly extruded stinger is visible. It is surrounded by long sensory setae (confirmed by histology; probably mechanoreceptors) on the edge of the pygidium and 7th sternum.

Below: Grooved cuticular structures on the pygidium associated with the pygidial gland. This structure is usually covered by the preceding 6th tergite.



glands. All ants following the trails to the end during a 5-minute period were counted.

As can be seen from table 1, trails drawn either with crushed pygidial glands or poison glands elicited a precise trail following behavior in all three worker castes (Fig. 6), but the ants did not respond to trails drawn with crushed Dufour's glands. We noticed, however, several differences in the reaction of the ants to poison gland trails and pygidial gland trails. (1) When both trails were offered simultaneously, starting at the periphery of a "homeless" colony, significantly more workers (Tab. 1) carrying brood moved along the poison gland trail. (2) In all tests the poison gland trail was the more effective one and lasted over a longer period of time. After 5 minutes the ants' response to pygidial gland trails had almost vanished, whereas they were still strongly following the trail drawn with poison gland material. In fact, poison gland trails presented to the ants 24 hours after they were drawn were still effective as orientation cues for emigrating *O. versicolor* workers. (3) Although we could not detect a preference for either trails drawn with poison glands or pygidial glands, ants moving along the pygidial gland trail seemed to gape their mandibles more frequently than ants moving along poison gland trails.

From these observations we conclude that the trail pheromones serve different functions. The poison gland trail is obviously employed during nest emigrations, where it serves as a stimulative recruitment signal as well as a longer lasting orientation cue. On the other hand, the pygidial gland trail probably functions as a relatively short lasting alarm-recruitment signal, channeling workers to areas of disturbance near the nest. It is also possible that the pygidial gland pheromone is discharged by successful foragers when they return to the nest, which might cause the social facilitation of the foraging activity mentioned above. In fact, when a crushed pygidial gland is presented inside the nest tube, it elicits more excitement in the workers than any other glandular secretions (mandibular gland, poison gland, Dufour's gland), causing several workers to move toward the nest entrance.

All three worker castes have the same glandular equipment and their secretions release the same behavioral responses.



Fig. 6. Trail test with *Orectognathus versicolor*. Artificial trails drawn with secretions from the poison gland (PoG) and Dufour's gland (C), both originating at the opening of the nest tube, are offered simultaneously. All workers follow the poison gland trail.

*Discussion:*

It has been well documented that many species of the sub-family Myrmicinae employ secretions from the glands associated with the sting apparatus (poison gland, Dufour's gland) for chemical trail communication and orientation (for review see Wilson 1971; Hölldobler 1978). This paper presents the first evidence of the phenomenon in the myrmicine tribe Dacetini.\*

In the dacetine species *Orectognathus versicolor* trails laid with poison gland secretions function both as recruitment and orientation signals during nest emigration. In fact, many dacetine species seem to construct relatively simple nests in soil or rotting wood and it is easily conceivable that colonies frequently abandon their nests and move to new nest sites. More surprising, however, was the discovery that this species possesses a pygidial gland whose structure closely resembles that of the pygidial gland of some ponerine species. The secretions of this gland can also function as a recruitment trail pheromone in *O. versicolor*.

Table 1. Number of workers following artificial trails within 5 min. periods. The means and standard deviations are given.

Trails presented at nest entrance (n = 4)					
Dufour's gland	water control	Poison gland	water control	Pygidial gland	water control
0	0	12.7 ± 3.8	0	8.3 ± 2.8	0
Trails presented simultaneously at periphery of clustered colony (n = 5)					
Dufour's gland		Poison gland		Pygidial gland	
with brood incl. males	without brood	with brood incl. males	without brood	with brood incl. males	without brood
0	0	7.8 ± 3.8	7.0 ± 2.2	2.0 ± 1.6	9.8 ± 3.1

\*Blum and Portocarrero (1966) demonstrated that three attine ant genera follow trails drawn with poison gland secretions of *Daceton armigerum*, but they could not demonstrate trail following behavior in *Daceton*.



From recent investigations we know that the pygidial gland is quite common in the Myrmicinae (Kugler 1978; Hölldobler and Engel 1978). In at least two species its secretions serve as an alarm pheromone (Hölldobler et al. 1976; Kugler 1979). On the other hand, in several ponerine species the pygidial gland secretions have been demonstrated to function as a recruitment pheromone during tandem running (Hölldobler and Traniello 1980a) or trail communication (Maschwitz and Schönege 1977; Hölldobler and Traniello 1980b). From our findings in *O. versicolor* it appears now that this ponerine trait might have been preserved in the Dacetini, whose origin presumably dates back to early Tertiary times (Brown and Wilson 1959). If this speculation is right, we should expect that the most primitive dacetine species, *Daceton armigerum* (Brown and Wilson 1959; Wilson 1962), has a well developed pygidial gland, resembling closely that found in many ponerine ants, and its secretions presumably serve as an alarm-recruitment pheromone. In fact, Wilson (1962) observed that workers of *D. armigerum* often moved to areas of excitement and when a worker just had discovered prey it moved in "excited broken running patterns" by which other ants in the vicinity might be attracted. Wilson (1962, 1971) hypothesized that this running pattern might serve as a communicative signal of the kind of "Stäger's kinopsis", i.e. the large-eyed *Daceton* workers might respond to the visual stimuli produced by the excitedly moving nestmate. We have now to consider the possibility that a *Daceton* huntress which pursues a prey, discharges a short-range recruitment pheromone from the pygidial gland, and that consequently the attraction of other huntresses in the close vicinity is caused by this chemical signal.

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## REFERENCES

- BLUM, M. S. AND C. A. PORTOCARRERO  
 1966 Chemical releases of social behavior. X. An attine trail substance in the venom of a non-trail laying myrmicine, *Daceton armigerum*. *Psyche* (Cambridge) **73**: 150-155.
- BROWN, W. L. AND E. O. WILSON  
 1959 The evolution of the dacetine ants. *Quarterly Rev. Biology* **34**, 278-294.
- CARLIN, N. F.  
 1982 Polymorphism and division of labor in the dacetine ant *Orectognathus versicolor* (Hymenoptera: Formicidae) *Psyche* (Cambridge) **88**:231-244.
- HÖLLDOBLER, B. AND H. ENGEL  
 1978 Tergal and sternal glands in ants. *Psyche* (Cambridge) **85**, 285-330.
- HÖLLDOBLER, B. AND J. TRANIELLO  
 1980a Tandem running pheromone in ponerine ants. *Naturwissenschaften* **67**, 360.
- HÖLLDOBLER, B. AND J. F. A. TRANIELLO  
 1980b The pygidial gland and chemical recruitment communication in *Pachycondyla* (= *Termitopone*) *laevigata*. *J. Chem. Ecology* **6**, 883-893.
- HÖLLDOBLER, B., R. STANTON AND H. ENGEL  
 1976 A new exocrine gland in *Novomessor* (Hymenoptera: Formicidae) and its possible significance as a taxonomic character. *Psyche* **83**, 32-41.
- KUGLER, C.  
 1978 Pygidial glands in the myrmicine ants (Hymenoptera: Formicidae). *Insectes sociaux* **25**, 267-274.
- 
- 1979 Alarm and defense: a function for the pygidial gland of the myrmicine ant, *Pheidole biconstricta*. *Annals Entomological Society America* **72**, 532-536.
- MASCHWITZ, U. AND P. SCHÖNEGGE  
 1977 Recruitment gland of *Leptogenys chinensis*. *Naturwissenschaften* **64**, 589-590.
- RATHMAYER, W.  
 1962 Methylmetacrylat als Einbettungsmedium für Insekten. *Experientia* (Basel) **18**, 47-48.
- ROMEIS, B.  
 1948 *Mikroskopische Technik*, München 1948.
- WILSON, E. O.  
 1962 Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in ants. *Bull. Mus. Comp. Zool. Harvard Univ.* **127**, 401-422.
- 
- 1971 *The insect societies*. The Belknap Press of Harvard University Press, Cambridge, Mass.